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Research article

Four *Achnanthidium* species (Bacillariophyta) formerly identified as *Achnanthidium minutissimum* from the Antarctic Region

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Abstract. Four taxa belonging to the complex of species around *Achnanthidium minutissimum* were found during the ongoing taxonomic revision of the Antarctic freshwater and limno-terrestrial diatom flora. Two taxa were previously described as *Achnanthidium lailae* and *A. sieminskae*. Two others were formerly identified as *A. minutissimum* but detailed light and scanning electron microscopical observations revealed sufficient morphological differences compared to the type of *A. minutissimum*, to justify their separation and description as new taxa: *Achnanthidium indistinctum* and *A. maritimo-antarcticum*. The morphology and ecology of all four taxa are discussed comparing the species with morphologically similar taxa. The biogeographical consequences of the splitting of the former *A. minutissimum* complex in the Antarctic Region are discussed.

Keywords. *Achnanthidium*, Bacillariophyta, Antarctic Region, new species, biogeography.

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Introduction

Based on the list of all published diatom records (40 entries) from the Antarctic Region in Kellogg & Kellogg (2002), *Achnanthes minutissima* Kütz. (Kützing 1833) is one of the most commonly observed diatom taxa in the (sub-)Antarctic Region. Apart from the Antarctic Continent, the species has been reported from all investigated localities on the sub-Antarctic Islands in the southern Indian Ocean (Bourrelly & Manguin 1954; Le Cohu 2005; Van de Vijver *et al.* 2002) and the Maritime Antarctic Region (e.g., South Shetland Islands, South Orkney Islands) (Jones *et al.* 1993; Oppenheim 1994). The species often forms large populations on the sub-Antarctic islands, dominating the aquatic diatom communities in lakes and pools (Van de Vijver *et al.* 2001, 2002, 2004, 2008). All findings contributed to the generally accepted idea that *A. minutissima* was a typical cosmopolitan species showing a worldwide distribution on all continents (Ector 2011).

The correct identity and biogeographical distribution of this taxon has for a long time been obscured by force-fitting and taxonomic drift. As a correct interpretation of the type of *A. minutissima* was virtually unknown, all identifications were based on the short description in Kützing (1833). In 1994, Czarnecki transferred the species to the genus *Achnanthidium* as *Achnanthidium minutissimum* (Kütz.) Czarnecki (Czarnecki 1994). The type material of *Achnanthes minutissima* remained unstudied until Potapova & Hamilton (2007) published for the first time several SEM images from the type material. Following a taxonomic workshop in Luxemburg in 2009 (Ector 2011), it was clear that the old concept of *A. minutissimum* was no longer acceptable and that a revision of all populations formerly identified as *A. minutissimum* was necessary. A special volume of Algological Studies (published in 2011) describing the workshop results, was entirely dedicated to the study of the *Achnanthidium minutissimum*-complex. A large number of new taxa were described, split off from the former catch-all taxon *A. minutissimum* and some of its varieties. Since 2009, more than 15 new *Achnanthidium* species have been described such as *A. caravelense* Novais & Ector (Novais *et al.* 2011), *A. acerosum* Van de Vijver, Lange-Bert. & Jarlman (Van de Vijver *et al.* 2011a) and *A. acsiae* Wojtal, E.Morales, Van de Vijver & Ector (Wojtal *et al.* 2011). Simultaneously to the revision of the European and North American *Achnanthidium minutissimum* complex, several Antarctic populations have been re-investigated which resulted in the separation of two new species with a purely Antarctic distribution. In 2009, Zidarova *et al.* described *Achnanthidium lailae* Van de Vijver (Zidarova *et al.* 2009) from James Ross Island located in the northern Weddell Sea, close to the Antarctic Peninsula. Three years later, *Achnanthidium sieminskae* Witkowski, Kulikovskiy & Riaux-Gobin (Witkowski *et al.* 2012) was described from the sub-Antarctic Iles Kerguelen in the southern Indian Ocean.

During a survey of the freshwater diatom flora from the Maritime Antarctic Region, two other taxa have been found that were previously identified as *A. minutissimum*. Analysis of their ultrastructure using scanning electron microscopy revealed significant differences with the type of *Achnanthidium minutissimum* and with all other recently split-off taxa justifying their description as new taxa. The present paper gives a formal description for both new taxa, *Achnanthidium maritimo-antarcticum* sp. nov. and *A. indistinctum* sp. nov., and discusses the morphology, ecology and distribution of the two other Antarctic taxa, *A. lailae* and *A. sieminskae*.

Material and methods

Samples used in this study were collected during several field trips from different aquatic habitats on the South Shetland Islands (Livingston Island), James Ross Island and the sub-Antarctic Islands in the southern Indian (Iles Crozet, Iles Kerguelen, Prince Edward Islands) and Atlantic Ocean (South Georgia) (Fig. 1). Details on sampling methods and physico-chemical analyses can be found in Van de Vijver & Beyens (1996), Van de Vijver *et al.* (2001, 2002, 2004, 2008), Kopalová *et al.* (2013) and Kopalová & Van de Vijver (2013).

Diatom samples for LM observation were prepared following the method described in Van der Werff (1955). In total, ten sampling sites from various Antarctic localities were examined in this study, with all samples listed in Table 1. Subsamples of the original material were oxidized using 37% H_2O_2 and heating to 80°C for approximately 1h. The reaction was further completed by the addition of KMnO4. Following digestion and centrifugation (three times 10 minutes at 3700x g), the material free of organic matter was diluted with distilled water for sample mounting to avoid excessive concentrations of diatom valves and frustules on the slides. A subsample from the organic-free material was mounted in Naphrax® for diatom community studies. The slides were analysed using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) and an Olympus UC30 digital camera. Samples and slides are stored at the BR-collection, property of the Belgian federal government and given in permanent loan to the Botanic Garden Meise (Belgium). For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1-µm Isopore™ polycarbonate membrane

filter (Merck Millipore). The stubs were sputter-coated with a Gold-Palladium layer of 10 nm and studied in a ZEISS ULTRA SEM microscope at 3 kV (Natural History Museum London, UK). Diatom terminology follows Ross *et al.* (1979), Round *et al.* (1990) and Potapova & Hamilton (2007). For comparison, the following publications were consulted: Krammer & Lange-Bertalot (1991), Kobayashi (1997), Potapova & Ponader (2004), Ivanov & Ector (2006), Potapova (2006), Monnier *et al.* (2007), Ponader & Potapova (2007), Potapova & Hamilton (2007), Zidarova *et al.* (2009), Hlúbiková *et al.* (2011), Morales *et al.* (2011), Van de Vijver *et al.* (2011a, 2011b) and Witkowski *et al.* (2012).

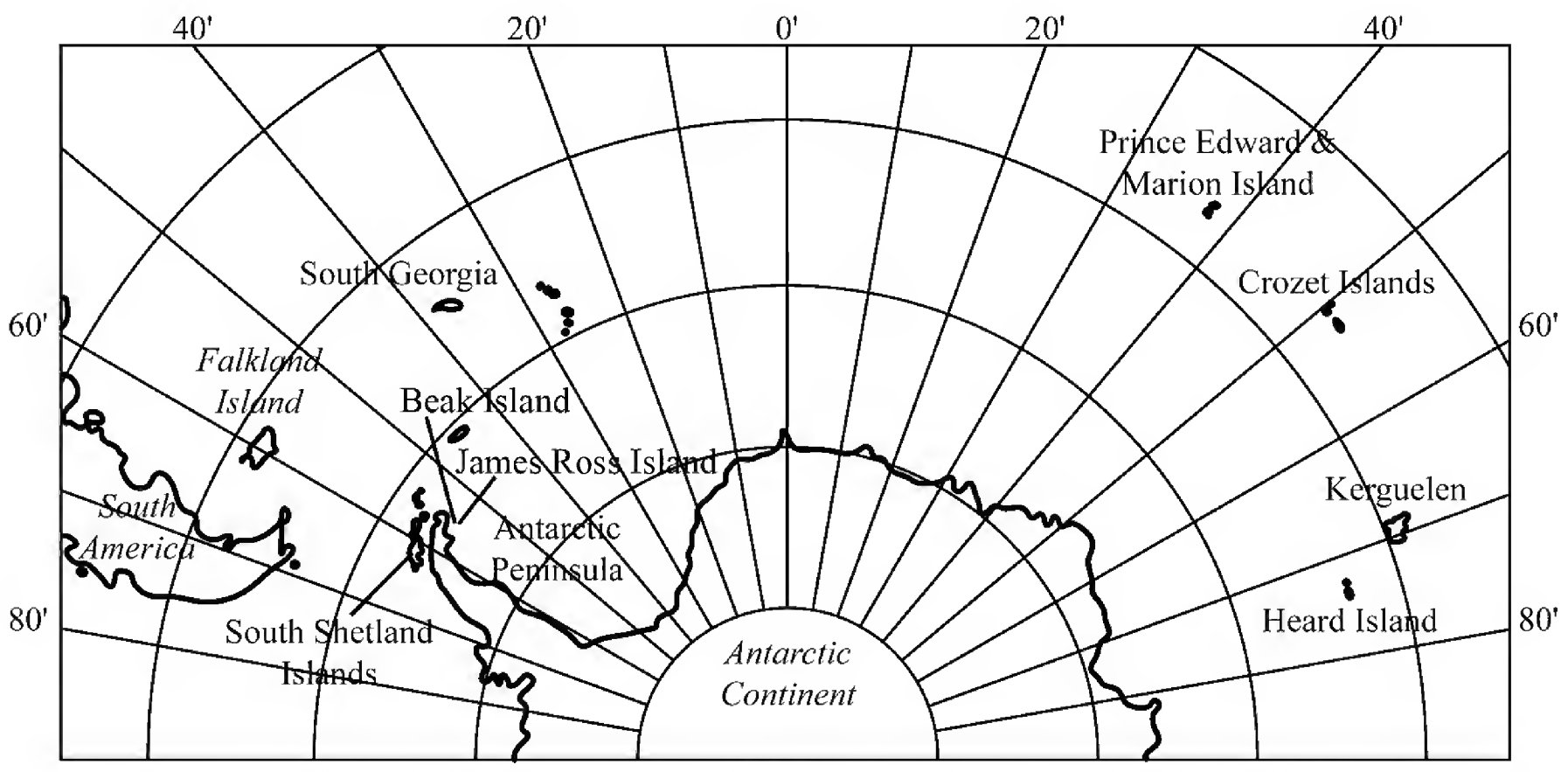


Fig. 1. The Antarctic region with the location of the sampled islands and archipelagos.

Table1. List of samples used in this study.

Sample ID	**Geographic locality**	**Source**
C-BW184	Crozet	Van de Vijver *et al.* (2002)
KER-POCO008	Kerguelen	this study
KER-BW417	Kerguelen	Van de Vijver *et al.* (2001)
He-D273	Heard Island	Van de Vijver *et al.* (2004)
PEI-D50	Prince Edward Islands	Van de Vijver *et al.* (2008)
SG-W398	South Georgia	Van de Vijver & Beyens (1996)
LIV-BYM051	Livingston Island	this study
LIV-BY055	Livingston Island	Kopalová & Van de Vijver (2013)
JRI2009-CLW58	James Ross Island	this study
JRI2009-CLW60	James Ross Island	this study

Results

Class Bacillariophyceae Haeckel emend. Medlin & Kaczmarska 2004 (Medlin & Kaczmarska 2004)
Subclass Bacillariophycidae D.G.Mann in Round et al. 1990 (Round et al. 1990)
Order Achnanthales Silva 1962 (Silva 1962)
Family Achnanthidiaceae D.G.Mann in Round et al. 1990 (Round et al. 1990)
Genus *Achnanthidium* Kütz. 1844 (Kützing 1844)

Achnanthidium indistinctum Van de Vijver & Kopalová sp. nov.
Figs 2-28

Morphological observations

Light microscopy (Figs 2-24)

Frustules short, rectangular in girdle view, bent around the transapical axis (Figs 2-4). Mantle striae often apparently thickened in LM (Fig. 4). Valves narrowly lanceolate with slightly to clearly convex margins and distinctly protracted, rostrate apices (Figs 2-24). Valve dimensions (n=30): length 8.5–13.0 µm, width 1.8–2.2 µm. Raphe valve (Figs 5-15) concave with a very narrow linear axial area, almost invisible towards the valve apices, almost not widening towards the central part of the valve. Central area very small, indistinct, bordered by several (usually two) more widely spaced striae. Raphe straight, filiform, almost invisible, with simple proximal raphe endings. Distal raphe fissures not discernible in LM. Striae moderately radiate throughout the entire valve, becoming indiscernible (due to higher density) near the apices. Rapheless valve (Figs 16-24) slightly convex with narrow, linear axial area, not or very slightly widening towards the valve centre. Central area almost non-existing, never forming a fascia or subfascia. Central striae very weakly more distantly spaced. Striae weakly radiate throughout, only very slightly more densely spaced near the apices, 30–35 in 10 µm.

Scanning electron microscopy (Figs 25-28)

Striae in the rapheless valve composed of a series of 3–4 distinct, rounded to square areolae (Fig. 25). Slit-like areolae apparently never present. Central striae less dense than in the rest of the valve (Fig. 25). Near the apices, striae only composed of 1–3 rounded areolae (Fig. 25). Mantle areolae elongated, slit-like, often enlarged (Fig. 25). Striae on the raphe valve, ca. 36 in 10 µm, composed of 2–3 irregularly shaped (mostly rounded or elongated rectangular) areolae (Fig. 26). Near the apices, stria density higher (up to 38 in 10 µm), composed of fewer areolae (Fig. 26). Internal areolae openings on both valves covered by hymenes (Figs 27, 28). External raphe branches straight terminating in simple, short proximal raphe endings (Fig. 26). Distal raphe fissures straight, terminating just beyond the last apical stria (Fig. 26). Internally, proximal raphe endings shortly bent into opposite directions (Fig. 28). Distal raphe endings terminating in small helictoglossae (Fig. 28).

Etymology

The specific epithet was given because the species is rather small and can be easily overlooked.

Type material

Holotype

Slide BR-4361 (National Botanic Garden, Meise, Belgium).

Isotypes

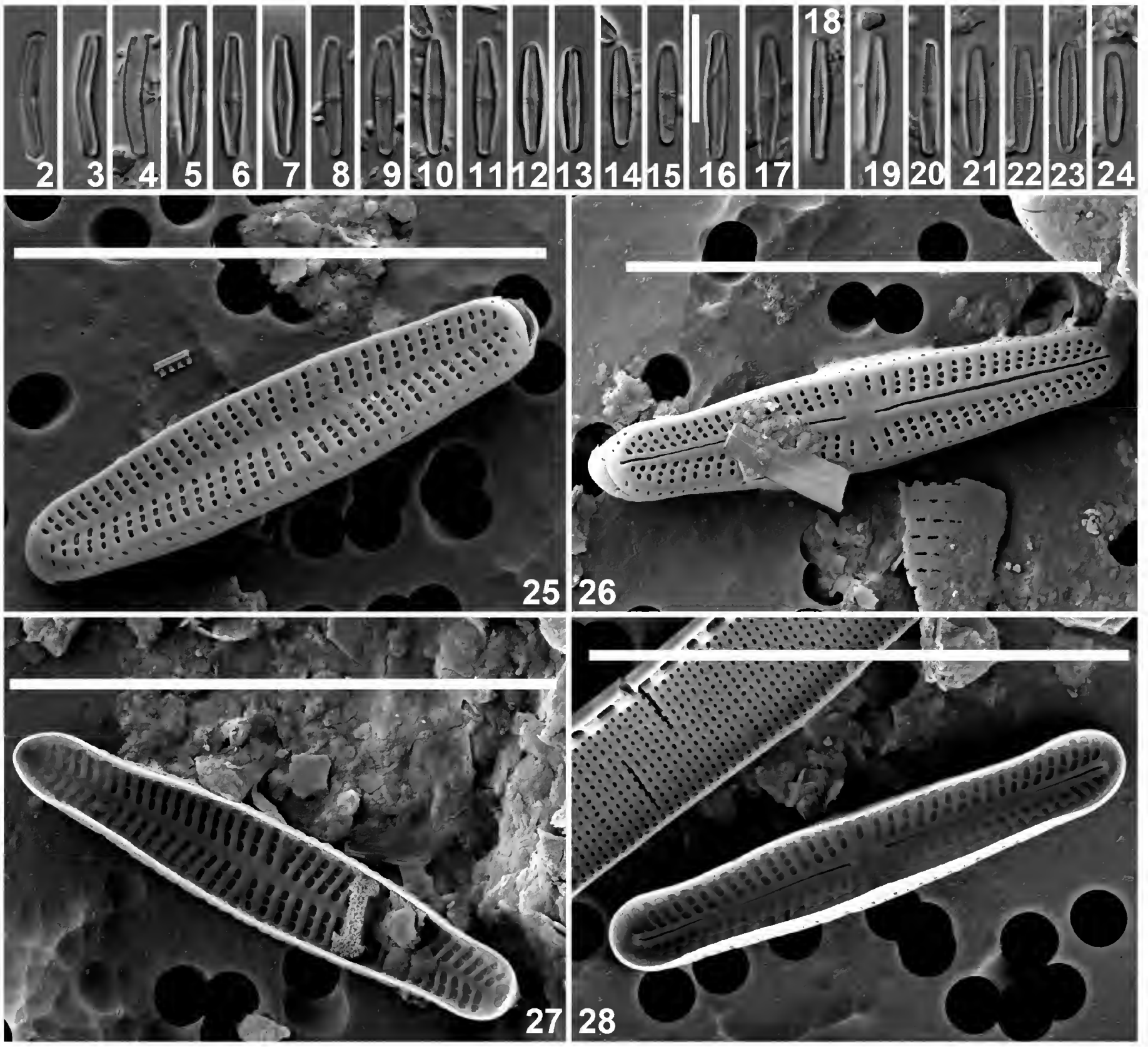
Slides PLP-251 (UA, University of Antwerp, Belgium).

Type locality

Byers Peninsula, Livingston Island, South Shetland Islands, sample BYM051 (62°38'20.1"S 61°06'44.2"W) (Leg. B. Van de Vijver; coll. date 15 Jan. 2009).

Ecology, distribution and associated diatom flora

So far, *A. indistinctum* has only been found on Livingston Island (South Shetland Islands). The type population was observed living on submerged mosses collected in a large lake on the central plateau, located between Midge Lake and Limnopolar lake. The lake had an alkaline pH (7.35) with a low specific conductance value (97 µS/cm) and a high phosphate level (5.2 mg/l). The flora in the sample was



Figs 2-28. *Achnanthidium indistinctum* Van de Vijver & Kopalová sp. nov. Light and scanning electron micrographs of the type population on Byers Peninsula (Livingston Island). **2-4**. LM views of some frustules in girdle view. **5-15**. LM views of raphe valves. **16-24**. LM views of rapheless valves. **25**. SEM external view of an entire rapheless valve. **26**. SEM external view of an entire raphe valve. **27**. SEM internal view of an entire rapheless valve. **28**. SEM internal view of an entire raphe valve. Scale bars represent 10 µm.

dominated by several *Psammothidium* species [*P. abundans* (Manguin) Bukht. & Round (Bukhtiyarova & Round 1996), *P. papilio* (D.E. Kellogg, M. Stuiver, T.B. Kellogg & G.H. Denton) Van de Vijver & Kopalová (Kopalová *et al.* 2012), *P. subatomoides* (Hust.) Bukht. & Round (Bukhtiyarova & Round 1996)], *Nitzschia* cf. *perminuta* (Grunow) M.Peragallo (Peragallo 1903), *Brachysira minor* (Krasske) Lange-Bert. *in* Lange-Bertalot & Moser (Lange-Bertalot & Moser 1994), *Sellaphora seminulum* (Grunow) D.G.Mann (Mann 1989) and *Amphora* sp. It is possible that the species is also present on Signy Island (South Orkney Islands) based on the illustrations in Oppenheim (1994). The distribution in the Antarctic region and other geographical areas is unclear due to the insufficient discrimination between species in the *Achnanthidium minutissimum*-complex. All published records should be verified in order to know the exact biogeography of this and all other taxa.

Achnanthidium maritimo-antarcticum Van de Vijver & Kopalová sp. nov.
Figs 29-53

Morphological observations

Light microscopy (Figs 29-49)

Frustules in girdle view rectangular, bent around the transapical axis (Figs 29, 30). Valves linear-lanceolate with parallel to slightly convex margins and clearly protracted, rostrate, occasionally subcapitate apices (Figs 31-49). Valve dimensions (n=25): length 12–15 µm, width 2.3–2.7 µm. Raphe valve (Figs 31-40) concave with a linear axial area, narrow to almost absent near the valve apices, hardly widening towards the central part of the valve. Central area irregular, formed by several more widely spaced striae. Raphe straight, filiform, invisible, with indistinct straight, simple proximal raphe endings. Distal raphe hardly discernible in LM. Striae slightly radiate throughout the entire valve, becoming more radiate and more densely spaced near the apices, 30– 33 in 10 µm, up to 40–42 in 10 µm near the valve apices. Rapheless valve (Figs 41-49) slightly convex with very narrow, linear axial area, widening to form a weakly elliptically, never transapically elongated central area, never forming a fascia or subfascia. Central striae slightly more distantly spaced. Striae slightly radiate throughout, only slightly more denser near the apices, 30–32 in 10 µm.

Scanning electron microscopy (Figs 50-53)

Striae in the raphe valve composed of a series of 3–4 distinct, rounded to square areolae terminating in one transapically elongated, rectangular areola (Fig. 50). Central striae composed of 2 rounded areolae and one transapically elongated areola near the valve margin (Fig. 50). Occasionally, short slit-like areolae interposed between the central striae. Near the apices, striae only composed of 2–3 rounded areolae (Fig. 50). Mantle areolae elongated, slit-like. Striae on the rapheless valve composed of 2–5 irregularly shaped (mostly rounded or elongated rectangular) areolae (Fig. 51). Near the apices, striae showing lowest number of areolae (Fig. 51). Internal areolae openings on both valves covered by hymenes (Figs 52, 53). External raphe branches straight to weakly curved terminating in simple, short proximal and distal raphe endings (Fig. 50). Distal raphe endings terminating just beyond the last apical stria (Fig. 50). Internally, proximal raphe endings short, slightly bent. Distal raphe endings terminating in small helictoglossae (Fig. 52).

Etymology

The specific epithet refers to the geographical area where the new species was found: Maritime Antarctic Region. The hyphen can and should be maintained in the species name based on art. 60.9 of the International Code of Nomenclature for algae, fungi and plants (McNeill *et al.* 2012).

Type material

Holotype

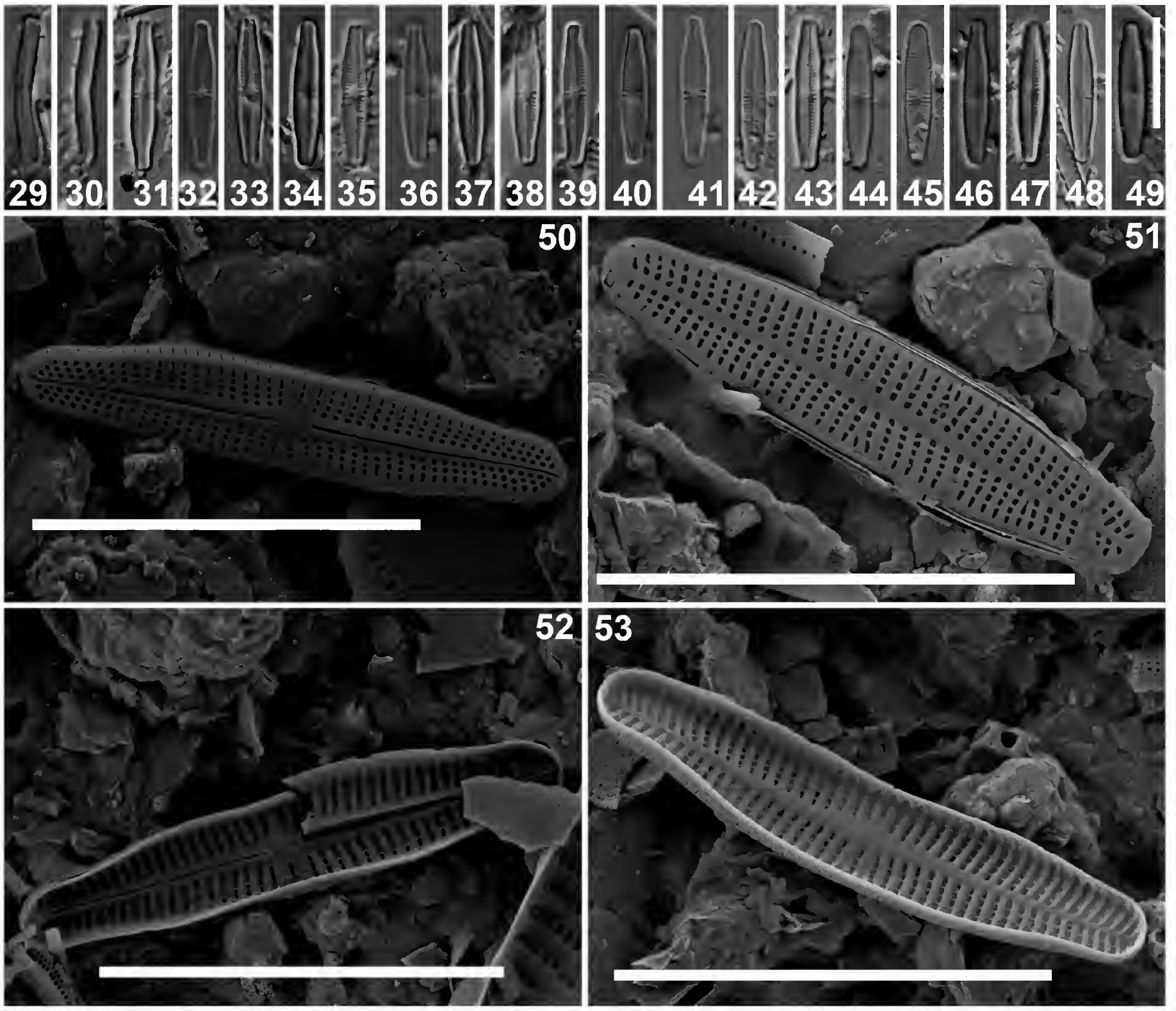
Slide BR-4362 (National Botanic Garden, Meise, Belgium).

Isotypes

Slides PLP-252 (UA, University of Antwerp, Belgium).

Type locality

Byers Peninsula, Livingston Island, South Shetland Islands, sample BY055 (62°37'41.7"S 61°06'30.4"W) (Leg. B. Van de Vijver; coll. date 15 Jan. 2009).



Figs 29-53. *Achnanthidium maritimo-antarcticum* Van de Vijver & Kopalová sp. nov. Light and scanning electron micrographs of the type population on Byers Peninsula (Livingston Island). **29-30**. LM views of some frustules in girdle view. **31-40**. LM views of raphe valves. **41-49**. LM views of rapheless valves. **50**. SEM external view of an entire raphe valve. **51**. SEM external view of an entire rapheless valve. **52**. SEM internal view of an entire raphe valve. **53**. SEM internal view of an entire rapheless valve. Scale bars represent 10 µm.

Ecology, distribution and associated diatom flora

The type population of *A. maritimo-antarcticum* was found in a large lake located on the central plateau of Byers Peninsula. The lake is characterized by a weakly alkaline pH (7.5) and a low conductivity (130 µS/cm). The ion composition in the lake is mainly dominated by Na^+ (20.0 mg/l) and Ca^{2+} (12.1mg/l). Both nutrients ($N\text{-}NO_3$+$N\text{-}NO_2$) and phosphate were rather low (25 µg/l and 10 µg/l resp.). The shoreline of the lake was completely covered with partly submerged mosses. Dominant taxa in the sample included *Fragilaria capucina* s.l. Desm. (Desmazières 1825), *Staurosirella* sp., *Navicula cremeri* Van de Vijver & Zidarova *in* Van de Vijver *et al.* (Van de Vijver *et al.* 2011d) and *Nitzschia* cf. *perminuta*. Smaller populations were found in other lakes such as Limnopolar Lake but these populations never exceed 1% of the total diatom composition. Due to force-fitting and taxonomic drift, the distribution of the new taxon in the Antarctic Region is unclear.

Achnanthidium lailae Van de Vijver *in* Zidarova *et al.* (Zidarova *et al.* 2009)
Figs 54-77

Morphological observations

Light microscopy (Figs 54-74)

Frustules in girdle view narrow, rectangular, bent around the transapical axis, apices weakly recurved (Figs 54-56).Valves linear to very slightly linear-lanceolate with almost parallel margins and non-protracted, broadly rounded, never rostrate or capitate apices (Figs 57-74). Valve dimensions (n=30): length 10–14 µm, valve width 1.8–2.5 µm. Raphe valve (Figs 57-64) concave with a rather narrow, linear to linear-lanceolate axial area, widening towards the central area. Central area forming a typical rectangular fascia. Shortened marginal striae occasionally present in the central area. Raphe straight to weakly undulating with inconspicuous straight proximal raphe endings. Distal raphe fissures not discernible in LM. Striae weakly but still distinctly radiate near the valve center, becoming more radiate near the apices, 30–33 in 10 µm. Rapheless valve (Figs 65-74) slightly convex with moderately broad, clearly lanceolate axial area, widening near the valve centre. Central area elongated, rhombic lanceolate, never expanding into a fascia due to several longer marginal striae in the central area. Striae parallel to weakly radiate near the valve centre, more radiate near the apices, 28–30 in 10 µm.

Scanning electron microscopy (Figs 75-77)

Striae on the raphe valve composed of 2–3 small areolae (Fig. 77). Areolae close to the axial area and at the apices rounded. Marginal areolae sometimes narrow, transapically elongated and hence slit-like, sometimes fused with the second areola (Fig. 77). Striae of the rapheless valve composed of 2–3 rounded to slit-like external areola openings (Fig. 75). Mantle areolae slit-like. Internal areolae openings covered by hymenes (Figs 76, 77). When removed due to sample preparation, very narrow struts visible separating the areolae (Fig. 76). Raphe slightly undulating becoming narrower towards the apices (Fig. 77). Proximal raphe endings almost straight, inconspicuous. Distal raphe fissures weakly deflected, continuing slightly beyond the last striae, never onto the mantle (Fig. 77). Internally, proximal raphe endings shortly bent into opposite directions, terminating in a thickened central pore (Fig. 77). Distal raphe endings terminating on small helictoglossae.

Ecology, distribution and associated diatom flora

The type population was found in a large circumneutral lake (pH = 7.1) on Ulu Peninsula on James Ross Island (Zidarova *et al.* 2009). Since then, several other large populations were discovered in lakes on Clearwater Mesa, a volcanic tableland on James Ross Island next to Ulu Peninsula. All populations were observed in alkaline lakes (pH 8.1–8.7) with relatively high conductivity (1000–2000 µS/cm). The samples were dominated by *Halamphora* sp., *Pinnularia australomicrostauron* Zidarova *et al.* (Zidarova *et al.* 2012), *Nitzschia* cf. *commutata* Grunow *in* Cleve & Grunow, and *Achnanthes coarctata* (Bréb.)

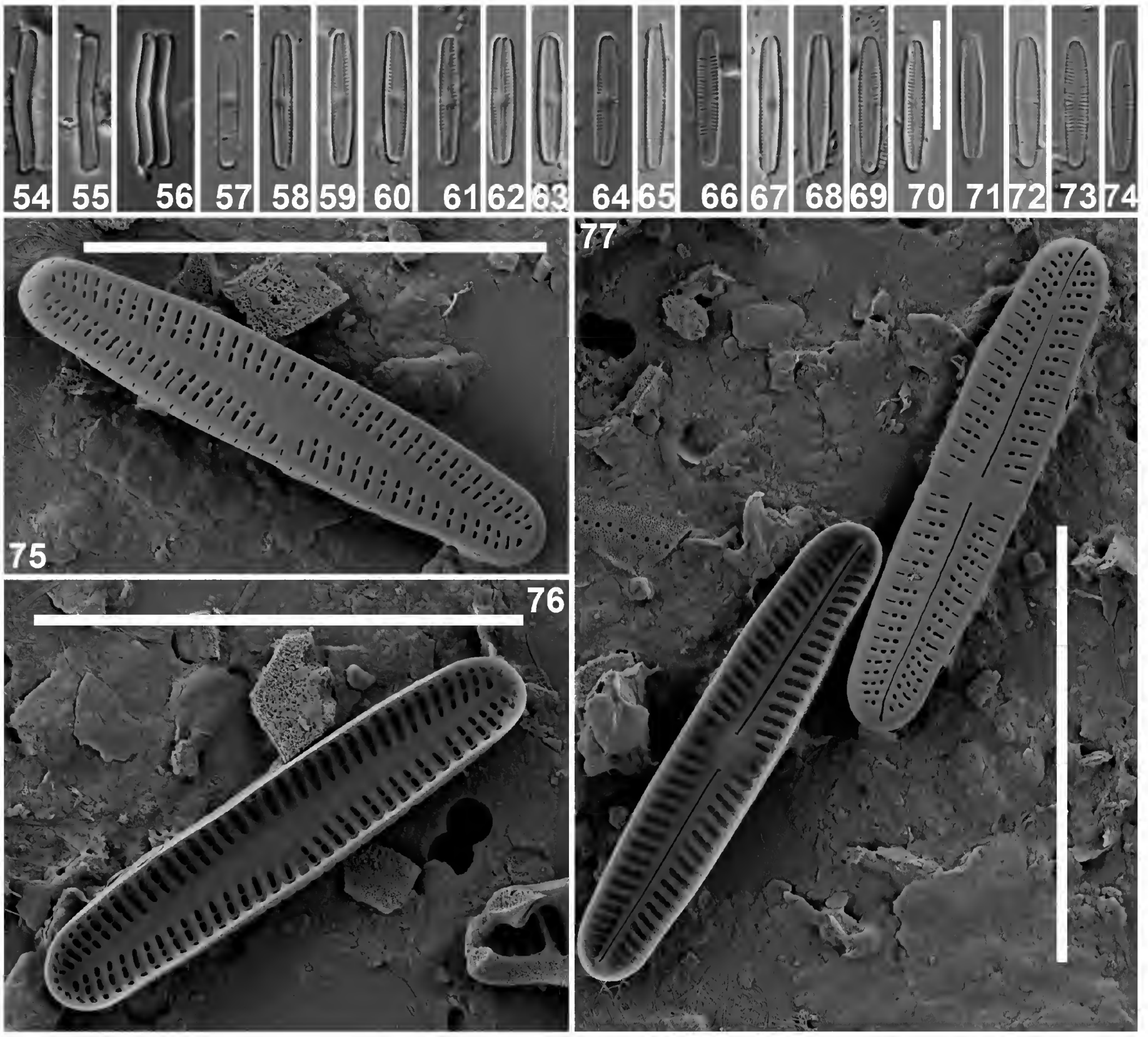
Grunow *in* Cleve & Grunow (Cleve & Grunow 1880) and *Gomphonema* sp. So far, no populations were found on other islands in the Maritime Antarctic Region (Kopalová & Van de Vijver 2013, Van de Vijver *et al.* unpubl. res.).

Achnanthidium sieminskae Witkowski, Kulikovskiy & Riaux-Gobin (Witkowski *et al.* 2012)
Figs 78-103

Morphological observations

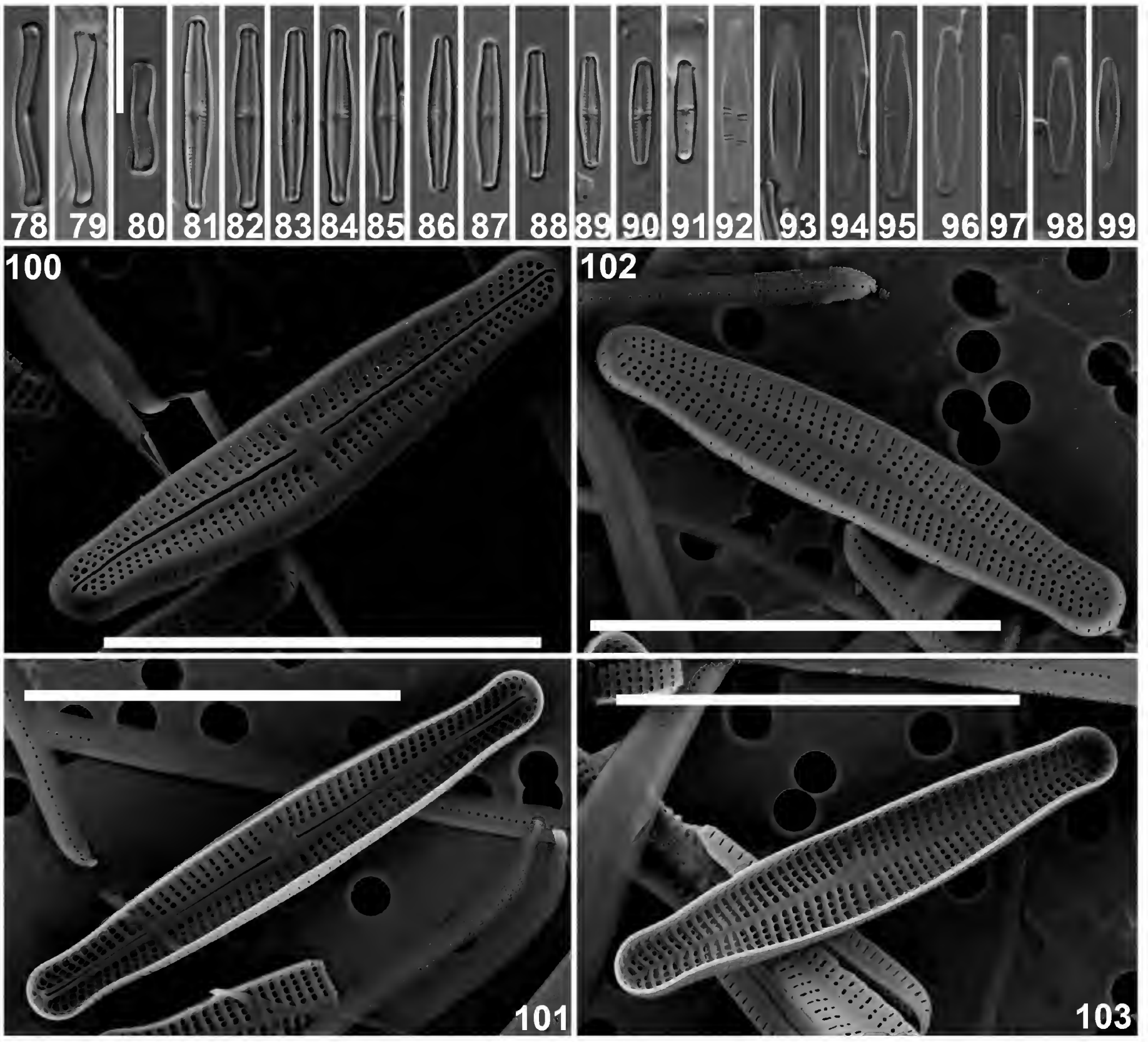
Light microscopy (Figs 78-99)

Frustules in girdle view rectangular, clearly bent around the transapical axis and with clearly recurved apices (Figs 78-80). Valves linear to narrowly linear-lanceolate with almost parallel to slightly convex



Figs 54-77. *Achnanthidium lailae* Van de Vijver. Light and scanning electron micrographs of a population on Clearwater Mesa (James Ross Island). **54-56**. LM views of some frustules in girdle view. **57-64**. LM views of raphe valves. **65-74**. LM views of rapheless valves. **75**. SEM external view of an entire rapheless valve. **76**. SEM internal view of an entire rapheless valve. **77**. SEM external (right) and internal (left) view of an entire raphe valve. Scale bars represent 10 μm.

margins and clearly protracted, rostrate to even capitate apices (Figs 81-99). Valve dimensions (n=25): length 9.5–18.0 µm, width 1.9–3.1 µm. Raphe valve (Figs 81-91) concave with a very narrow linear axial area, almost not discernible near the valve apices. Central area elliptical to rounded, very small, almost indistinct, formed by 2–3 more widely spaced striae. Central striae often lacking extending the central area up to the valve margin. Raphe straight, filiform with simple, straight proximal raphe endings. Distal raphe hardly discernible in LM. Striae weakly radiate near the valve center, becoming parallel and even convergent near the apices, well visible in LM, ca. 32 in 10 µm, more densely spaced near the valve ends. Rapheless valve (Figs 92-99) slightly convex with narrow, linear axial area, widening to form a weakly elliptically, never transapically elongated central area. Fascia never present. Central 2–3 striae more distantly spaced. Striae weakly radiate throughout, becoming more parallel to even convergent near the apices, ca. 35 in 10 µm.



Figs 78-103. *Achnanthidium sieminskae* Witkowski, Kulikovskiy & Riaux-Gobin. Light and scanning electron micrographs of a population on Iles Kerguelen. **78-80**. LM views of some frustules in girdle view. **81-91**. LM views of raphe valves. **92-99**. LM views of rapheless valves. **100**. SEM external view of an entire raphe valve. **101**. SEM internal view of an entire raphe valve. **102**. SEM external view of an entire rapheless valve. **103**. SEM internal view of an entire rapheless valve. Scale bars represent 10 µm.

Scanning electron microscopy (Figs 100-103)

Valve face of the raphe valve clearly concave. Valve face/mantle margin forming a weakly raised hyaline border separating valve face striae from mantle areolae. Striae, ca. 32–34 in 10 µm, composed of 2–3 small, rounded areolae (Fig. 100) followed near the valve center by a thin, slit-like, marginal areola (Fig. 100). Near the apices, striae more dense, ca. 40 in 10 µm, composed of only 3 rounded areolae. Mantle areolae slit-like (Figs 100, 102). Raphe almost straight with simple, straight proximal raphe endings (Fig. 100). Distal raphe fissures weakly deflected, continuing slightly beyond the last striae terminating on the valve face/mantle junction. Internally, proximal raphe endings shortly bent into opposite directions(Fig. 101). Distal raphe endings terminating in small helictoglossae (Fig. 101). Internal areolae openings covered by hymenes (Fig. 101). Striae of the rapheless valve almost equally spaced throughout the entire valve, 34–36 in 10 µm, composed of 2–5 rounded areolae sometimes terminating in one slit-like areola (Fig. 102). Mantle areolae slit-like. Internal areolae openings covered by hymenes (Fig. 103).

Ecology, distribution and associated diatom flora

Achnanthidium sieminskae was originally described as a brackish-littoral taxon from a tidal flat near the Kerguelen Islands (Witkowski *et al.* 2012) but the authors already expressed some doubts about this observation. Most likely, their population was the result of a riverine deposition in the marine Bossière fjord on Kerguelen. As they stated themselves, the only way to find out would be the analysis of the living material which was unfortunately no longer available at the time of their publication. We reported this taxon (as *A. minutissimum*) from a large number of purely freshwater habitats ranging from small pools to larger lakes and even streams from all sub-Antarctic islands in both the Indian and Atlantic Ocean (Van de Vijver & Beyens 1996; Van de Vijver *et al.* 2001, 2002, 2004, 2008). In many cases, very large populations could be observed, occasionally up to 60–80% of all counted valves. These data indicate that this is typical limno-terrestrial taxon preferring wet moss vegetations in pools, bogponds and lakes with a pH between 5.2 and 7.4 and a low conductivity (< 160 µS/cm). These data confirm the final conclusion in Witkowski *et al.* (2012) that the observed valves in their study are the result of the redeposition of a freshwater species in a marine environment. Given the large amount of available data and material, it is a pity the original authors did not verify their rather unusual observation more carefully.

Discussion

All taxa discussed here clearly belong to the complex of species around *Achnanthidium minutissimum* based on the simple, straight distal raphe endings contrary to the species in the *A. pyrenaicum* group that have clearly deflected to even hooked distal raphe fissures (Kobayashi 1997; Potapova & Hamilton 2007). In the (even recent) past, all taxa discussed were identified as *Achnanthidium minutissimum* (e.g., Oppenheim 1994; Van de Vijver *et al.* 2002; Le Cohu 2005; Kopalová & Van de Vijver 2013). Table 2 summarizes all important morphological features of all four taxa formerly identified as *A. minutissimum*. The application of a more fine-grained taxonomy based on a narrow species concept (Mann 1999), the detailed analysis of type material of so-called cosmopolitan taxa and as a consequence no longer force-fitting (Tyler 1996) and taxonomic drift, clearly influenced our understanding of the biogeography of Antarctic diatoms as shown in the taxonomic revision of several genera such as *Muelleria* (Van de Vijver *et al.* 2010), *Luticola* (Van de Vijver & Mataloni 2008, Van de Vijver *et al.* 2011c), *Hantzschia* (Zidarova *et al.* 2010) and *Navicula* (Van de Vijver *et al.* 2011d). A similar conclusion can now be made for the genus *Achnanthidium* confirming once more the unique nature of the Antarctic diatom flora and contradicting the Ubiquity hypothesis (Finlay & Clarke 1999) stating the cosmopolitan nature of all micro-organisms. As a consequence, the genus *Achnanthidium* shows some interesting biogeographical aspects. At present, only six *Achnanthidium* taxa are known from the Antarctic Region. Apart from the four taxa discussed in this paper, two other *Achnanthidium* taxa, *Achnanthidium modestiforme* (Lange-

Table 2. Overview of the main morphological features of all four taxa formerly identified as *A. minutissimum s.l.* reported from the Antarctic Region.

	A. indistinctum	***A. maritimo-antarcticum***	***A. lailae***	***A. sieminskae***
Valve length (µm)	8.5–13	12–15	10–14	9.5–18
Valve width (µm)	1.8–2.2	2.3–2.7	1.8–2.5	1.9–3.1
valve outline	narrowly lanceolate	linear-lanceolate	linear to very slightly linear-lanceolate	linear to narrowly linear-lanceolate
apices	distinctly protracted, rostrate	clearly protracted, rostrate, occasionally subcapitate	non-protracted, broadly rounded, never rostrate or capitate	clearly protracted, rostrate to even capitate
Rapheless valve				
# striae in 10 µm	30–35	30–32	28–30	ca. 35
# areolae per stria	3-4, rounded to rectangular	2–5, irregularly shaped	2-3, rounded to slit-like	2-5, rounded + sometimes 1 slit-like
striation pattern	slightly radiate throughout	slightly radiate throughout	parallel to weakly radiate near the valve centre, more radiate near the apices	Striae weakly radiate throughout, becoming more parallel to even convergent near the apices
Raphe valve				
# striae in 10 µm	ca. 36	30–33, up to 40–42 near the valve apices	30–33	ca. 32–34
# areolae per stria	2–3	2–3, rounded	2–3, small	2–3, small, rounded,+ near the valve center 1 slit-like
striation pattern	moderately radiate throughoout	slightly radiate throughout, more radiate towards the apices	weakly but still distinctly radiate near the valve center, becoming more radiate near the apices	weakly radiate near the valve center, becoming parallel and even convergent near the apices
(sub-)Antarctic distribution	South Shetland Islands	South Shetland Islands	James Ross Island	South Georgia, Prince Edward Islands, Iles Crozet, Iles Kerguelen, Heard Island

Bert.) Van de Vijver *in* Van de Vijver *et al.* (Van de Vijver *et al.* 2002) and *A. australexiguum* Van de Vijver *in* Taylor *et al.* (Taylor *et al.* 2014), a taxon recently described in the complex of species around *A. exiguum* (Grunow) Czarnecki (Czarnecki 1994), were confirmed from the Region. All six taxa are so far exclusively found in the Antarctic Region despite records of *A. modestiforme* from Argentina, Bolivia, Brazil and Chile (Maidana 1996; Díaz Villanueva & Maidana 1999; Rumrich *et al.* 2000; Tremarin *et al.* 2009; Morales *et al.* 2011) that are clear examples of force-fitting and most likely represent other, yet undescribed taxa. Two of these six taxa have a distribution that is at present only restricted to the sub-Antarctic Region (including all islands and archipelagos in the southern Indian Ocean and South Georgia in the southern Atlantic Ocean): *A. sieminskae* and *A. modestiforme*, lacking at present any confirmed records from other parts of the Antarctic Region. On the other hand, the Maritime Antarctic Region counts four *Achnanthidium* taxa (*A. lailae*, *A. maritimo-antarcticum* sp. nov., *A. indistinctum* sp. nov. and *A. australexiguum*), all of which so far never observed outside this Region. It is however unclear whether this biogeography represents the complete distribution of these taxa or is just the consequence of undersampling and underreporting. Kellogg & Kellogg (2002) list almost 40 records of *Achnanthidium minutissimum* (usually as *Achnanthes minutissima*) from mostly the Maritime Antarctic Region. All records should be verified to complete our biogeographical knowledge of the species discussed in this paper. Most literature records lack however (good) illustrations and even the retrieval of the original material is not always very straightforward making new sampling in these areas a more obvious choice to clarify the biogeography of these taxa.

Although molecular data would be interesting to confirm the separation of the taxa of the *A. minutissimum* complex, it is clear that all taxa discussed here are morphologically distinct from each other andare not conspecific with the former catch-all taxon *A. minutissimum*. Potapova & Hamilton (2007) already presented some SEM images of the type material of *A. minutissimum* s.s. Based on these published images and additional (but so far unpublished) observations on the type material of *A. minutissimum* (Novais *et al.* submitted), it is clear that none of the observed populations in the Antarctic Region represent *A. minutissimum* s.s.

Achnanthidium indistinctum can be separated from *A. minutissimum* based on several features (Potapova & Hamilton 2007; Hlúbiková *et al.* 2011). Morphometrically, *A. indistinctum* has clearly narrower valves (1.8–2.2 µm vs. 2.5–3.1 µm in *A. minutissimum*). Additionally, *A. minutissimum* has a higher number of areolae per stria, usually 4–5 (Novais *et al.* submitted), a high number never observed in *A. indistinctum* where 2–3(–4) is the rule. The mantle areolae in *A. indistinctum* are often enlarged making them easily visible in LM on frustules in girdle view, similarly to for instance *A. hoffmannii* Van de Vijver *et al.* (Van de Vijver *et al.* 2011a). Finally, the valve outline of *A. minutissimum* shows a combination of more convex valve margins together with clearly rostrate to subcapitate apices, compared to the weakly compared convex margins and weakly rostrate margins in *A. indistinctum*.

The second new taxon, *A. maritimo-antarcticum* can be separated from all other *Achnanthidium* taxa by its more linear valve outline in combination with the protracted, broadly rounded apices. The striae are solely composed of rounded to transapically elongated areolae, never presenting slit-like areolae as often found in several *Achnanthidium* taxa such as *A. hoffmannii*, *A. minutissimum* and *A. lailae*.

Zidarova *et al.* (2009) already discussed the differences between *A. lailae*, *A. minutissimum* and several other narrow, linear *Achnanthidium* taxa such as *A. strictum* Reichardt (Reichardt 2004) and *A. lineare* W.Sm. (Smith 1855). The analysis of additional populations of *A. lailae* on Clearwater Mesa, James Ross Island, confirm entirely the original separation of this taxon from the above mentioned taxa *A. minutissimum*, *A. strictum* and *A. lineare*, based on the weakly deflected distal raphe fissures and the higher number of areolae per stria in *A. lailae*. The only feature that need to be adjusted compared

to the original description, is the presence of slit-like areolae near the valve margins. In the original description, the absence of these slit-like areolae was mentioned (Zidarova *et al.* 2009).

Our observations on the often very large freshwater populations of *Achnanthidium sieminskae* from Iles Kerguelen refine our knowledge on the morphology of this species. According to the original description (Witkowski *et al.* 2012), the number of areolae per stria on the rapheless valve was set to 3, sometimes 2 areolae although in the accompanying table, 3–5 areolae are mentioned. Based on our results, and a more careful reanalysis of the illustrations in Witkowski *et al.* (2012), it is clear that the striae are composed of 2–5 rounded, sometimes slit-like areolae. Moreover, the populations observed on Iles Kerguelen and the other sub-Antarctic islands in the southern Indian Ocean, fine-tuned the morphometric data for this species. The observed length and width range in the freshwater and limno-terrestrial populations is larger than in the original description. Some raphe valves seem to lack one or two striae in the central area. The typical presence of 1–2 striae in the central area of *A. sieminskae* was used by Witkowski *et al.* (2012) as a discriminating feature to separate the species from *A. minutissimum*. It is clear that this feature should no longer be used. The separation of both taxa can also no longer be based on the denser striae near the apices as analysis of the Kützing type material of *A. minutissimum* (Novais *et al.* submitted) showed the presence of dense striae near the apices in the latter. Conspecificity of both taxa is however to be excluded but the separation of both taxa is therefore only possible based on the valve outline with more linear to linear-lanceolate valves (contrary to the typical lanceolate valves in *A. minutissimum*), the presence of clearly rostrate to capitate apices and differences in the number of areolae on the rapheless valve. In their analysis of the type of *A. minutissimum*, Novais *et al.* (submitted) show a rapheless valve having at least 5–6 rounded to weakly elongated areolae per stria whereas in the *A. sieminskae* valves shown in this paper, only 2–3(–4) rounded and one slit-like areola are shown. It is also clear that the raphe in *A. sieminskae* is usually more distinctly visible in LM than in *A. minutissimum*. *Achnanthidium sieminskae* shows some similarity to a few other (usually recently described) *Achnanthidium* taxa. Witkowski *et al.* (2012) compared their new species with *A. jackii* Rabenh. (Rabenhorst 1861) and *A. lailae*, although any confusion with the latter is entirely to be excluded based on valve outline, dimensions and stria structure. *Achnanthidium ertzii* Van de Vijver & Lange-Bert. *in* Van de Vijver *et al.* (Van de Vijver *et al.* 2011a), described from Madeira, shows a similar elongated valve outline but has narrower valves with a lower number of areolae per stria (2–3 vs. 3–5 in *A. sieminskae*) making conspecificity highly unlikely. *Achnanthidium maritimo-antarcticum*, described in this paper, has comparable valve dimensions but a more linear-lanceolate valve outline (compared to the typical lanceolate outline in *A. sieminskae*), a lower number of areolae per stria (max. 3) and less protracted, rostrate to subcapitate apices. The correct taxonomic and morphological identity of other *Achnanthidium* taxa such as *A. caledonicum* (Lange-Bert.) J.E.Slate & R.J.Stevenson (Slate & Stevenson 2007) is at present unclear making a comparison between *A. sieminskae* and these taxa rather difficult. *Achnanthidium caledonicum* as it is currently known, is much longer and has clearly capitate apices.

Conclusions

The present paper highlights the need for thorough morphological revisions of the entire Antarctic freshwater and limno-terrestrial diatom flora applying a narrower species concept. The description of two new *Achnanthidium* taxa split off from *Achnanthidium minutissimum* s.l. improves our knowledge about the biogeography of species in this complex and allows their use in more precise ecological and biogeographical studies.

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